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A NEW SPECIES OF *CASTILLEJA* (OROBANCHACEAE) FROM THE PÁRAMOS OF THE COLOMBIAN EASTERN CORDILLERA, WITH COMMENTS ON ITS ASSOCIATION WITH *PLANTAGO RIGIDA* (PLANTAGINACEAE)

Una especie nueva de *Castilleja* (Orobanchaceae) de los páramos de la cordillera Oriental de Colombia, con comentarios acerca de su asociación con *Plantago rigida* (Plantaginaceae)

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ABSTRACT

Castilleja paramensis F. González & Pabón-Mora, a perennial species of small herbs from páramos of Santander, Boyacá and Cundinamarca, in the Colombian Eastern Cordillera, is described and fully illustrated by photographs of the type collection. The new species is morphologically and ecologically similar to *C. nubigena, C. pumila*, and *C. virgata*, three perennial high Andean species from Ecuador, Peru and northern Chile and Argentina. *C. paramensis* is clearly distinguished from its relatives by the small size of the individuals, the broadly elliptic leaves and bracts (which are entire to slightly trilobed), the short (< 1 mm) pedicel, the small size (0.8-1.15 cm long) of the flowers, the not inflated calyx with the distal half bright yellow, the corolla often included to slightly exserted from the calyx, and the included style and stigma. The included corolla, stamens, styles and stigmas in *C. paramensis* strongly suggest the occurrence of cleistogamy. The new species often grows as a root hemiparasite of *Plantago rigida*.

Key words. High Andean flora, flora of Colombia, hemiparasitic plants, horizontal gene transfer, páramo endemics, root hemiparasites.

RESUMEN

Castilleja paramensis F. González & Pabón-Mora, una especie de hierbas perennes pequeñas propias de páramos de Santander, Boyacá y Cundinamarca, en la Cordillera Oriental Colombiana, es descrita y detalladamente ilustrada con fotografías de la colección tipo. La especie nueva es morfológica- y ecológicamente similar a *C. nubigena, C. pumila* y *C. virgata*, tres especies perennes de zonas altoandinas de Ecuador, Perú y norte de Chile y Argentina. *Castilleja paramensis* se distingue claramente de sus especies afines por el tamaño pequeño de los individuos, las hojas y las brácteas ancho-elípticas (las cuales son enteras a levemente 3-lobadas), el pedicelo extremadamente corto (< 1 mm), el tamaño reducido de las flores (0.8-1.15 cm largo), el cáliz no inflado, con la mitad distal de color amarillo brillante, la corola generalmente inserta o muy poco exerta del cáliz, y el estilo y estigma insertos. La

corola, los estambres y los estigmas insertos en *C. paramensis* sugieren la ocurrencia de cleistogamia. La nueva especie se encuentra frecuentemente como hemiparásita de raíces de *Plantago rigida*.

Palabras clave. Endemismos de páramo, flora altoandina, flora de Colombia, hemiparásitos de raíces, plantas hemiparasíticas, transferencia horizontal de genes.

INTRODUCTION

Castilleja Mutis ex L. f. comprises approximately 200 species (Holmgren 1978, Chuang & Heckard 1991, Heide-Jørgensen 2008) most of which are native to western North America. The South American species (estimated between 15 and 20; Egger, pers. comm.) are concentrated in the Andes. During the ongoing study of parasitic and hemiparasitic plants in Colombia by the authors, a number of specimens of *Castilleja* collected in the páramos of the Eastern Cordillera drew our attention because of the small size of the individuals and the frequent association with *Plantago rigida* Kunth. A specimen recently collected by FG in the páramo of Siscunsí (Sogamoso, Boyacá) matches all the morphological and ecological traits of the small-sized individuals previously collected in similar páramos of Santander, northern Boyacá, and Cundinamarca, in the Colombian Eastern Cordillera. Until now, these specimens have remained either undeterminated or were tentatively identified as infraspecific taxa of *C. fissifolia* L. f. or assigned to *C. nubigena* Kunth, a species known from the high Andes of Ecuador and Peru (cf. Holmgren 1984, Luteyn 1999, Molau, 1999). A detailed examination of these collections reveals, however, that they do not match any of the previously described species of *Castilleja* from Costa Rica/Panama (cf. Holmgren 1978) Venezuela (cf. Pennell 1953, Egger 2009), Colombia (cf. Fernández-Alonso 1987), Ecuador (cf. Holmgren 1984) or Peru (cf. Weddell 1857, Herrera 1926, Edwin, 1971). Thus, here we describe the new species and compare it with other high Andean species of *Castilleja* characterized by the small size of the individuals. Besides the disjunct distribution between the new species and the other morphologically similar high Andean species (*C. nubigena, C. pumila* (Benth.) Wedd. ex Herrera, *and C. virgata* (Wedd.) Edwin), the newly described species possesses clear-cut differences in the size and overall morphology of leaves, bracts, and flowers (Table 1).

Additionally, we include preliminary observations on the association of the species with *Plantago rigida*, as root hemiparasitism and hence physical plant interactions may also have genetic implications, for instance the occurrence of Horizontal Gene Transfer (HGT).

HGT has been reported between members of the Orobanchaceae and Plantaginaceae, preferentially involving mitochondrial and ribosomal over plastid genes (Mower *et al.* 2004, Davis & Wurdack 2004). For instance, the mitochondrial *atp1* has been transferred from *Bartsia* (Orobanchaceae) to *Plantago* (Mower *et al.* 2004). Plastid HGT seemed to have occurred less frequently, like between the parasitic *Orobanche* and *Pelipanche* (Park *et al.* 2007). These are both non-photosynthetic parasites with a shared plastid region including *rps2*, *trnL-F*, and *rbcL* that has probably been transferred *via* their common host (Park *et al.* 2007). At this point the genetic consequences of the *Castilleja paramensis*-*Plantago rigida* association are still unknown; however, their tight physical link and their exclusive distributions in high altitudes in the Andes, make them an excellent candidate to undertake studies testing explicitly for the occurrence of HGT.

Table 1. Comparative traits of *Castilleja paramensis* and the three high-Andean small perennial herbaceous species.

[1]Based on Kunth (1817), Holmgren (1984), and the specimens *Maguire & Maguire 61725* (fl, fr), collected in Ecuador, Bolívar, 3900 m, 18 Sep 1969 (COL), and *Barclay & Juajibioy 9174*, collected in Ecuador, Napo-Pastaza, 30 Aug 1959 (COL). [2]Based on Edwin (1971) and Holmgren (1984). [3]Based on Edwin (1971), and Holmgren (1984), and the holotype (available at http://plants.jstor.org/specimen/p00587597) and the specimen *Barclay 8365* (fl), collected in Ecuador, Azuay, 3400 m, 30 Jul 1959 (COL).

	***C. paramensis* sp. nov.**	***C. nubigena* Kunth[1]**	***C. pumila* (Benth.) Wedd.[2]**	***C. virgata* (Wedd.) Edwin[3]**
Habit	decumbent herbs, with ascending stems to 5(-8) cm tall; leaves sub-opposite and very congested	erect subshrubs, stems diffuse, 10-18.4 cm tall; leaves alternate, not congested	decumbent herbs, stems to 9 cm tall; leaves alternate, not congested	erect herbs or subshrub, 20-40(-60) cm tall; leaves alternate, not congested
Shape and size of leaf blade	broadly elliptic, to 0.7 x 0.5 cm	linear to lanceolate, trifid, 1.1-2.5 x 0.3-0.6 cm	lanceolate to broadly lanceolate, 0.7-2(-3.5) x 0.4-0.8 cm long	linear to lanceolate, 1.5-3(-4) x 0.3-0.5 cm
Number and shape of lateral lobes of the leaf	0-1 pair, broad	1-2 pairs, narrow	1-2(3) pairs, narrow	1-3 pairs, narrow
Shape and color of the bracts	broadly elliptic, entire or with 1 or 2 broad lateral lobes, bright red when young, then purplish	lanceolate to broadly lanceolate, deeply 3-5-lobate, red tipped	leaf-like, with 1-3 narrow lateral lobes, greenish or purple	leaf-like, with 1-3 narrow lateral lobes, green, tipped with red or rarely yellow
Length of the pedicel	< 1 mm	2-4 mm	1-2 mm	5-10 mm
Total length of the flower	0.8-1.15 cm	1.55-2 cm	1.5-2.2 cm	1.6-3.4 cm
Calyx *versus* corolla	corolla included or very slightly (for < 2 mm) exserted from the calyx	corolla exserted from the calyx for >4 mm	corolla exserted from the calyx for >4 mm	corolla exserted from the calyx for >4 mm
Color of the calyx	bright yellow at least in the marginal zone	red to occasionally purplish	reddish with green or pale green veins	pale green and dark green to purple tips
Shape and length of the calyx	not inflated, 8-11 mm	inflated, 11-16 mm long	basally inflated, 12-16(-19) mm	slightly inflated towards its middle zone, (12-)18-30 mm
Adaxial and abaxial clefts of the calyx	very unequal, the adaxial 1-1.5 mm, the abaxial 4.5-5.5 mm	very unequal, the adaxial 1-3 mm deep, the abaxial (6-)10-14 mm deep	subequal, the adaxial 3-5 mm deep, the abaxial 5-6.5 mm deep	very unequal, the adaxial 1-3 mm deep, the abaxial 6-11(-14) mm deep
Lateral clefts of the calyx	absent	present, to 1 mm deep	present, to 1 mm deep	absent
Color of the corolla	uniformly bright green	greenish	yellow green with purplish margins	Yellow green, sometimes orange along the margin of the galea
Length and shape of corolla	8-11.5 mm, straight to very slightly incurved	10-15(-20) mm, strongly incurved especially between the tube and the lobes	15-22(-26) mm. slightly curved outwards	(14-)16-23-(34) mm, slightly incurved
Length of the corolla tube	5-6 mm, usually longer than the galea	6-7 mm, approximately as long as the galea	8-16 mm, longer than the galea	8-12 mm, longer than the galea
Length of the galea	4-5.5 mm	4-9 mm	6-10 mm	6-11(-19) mm
Stamens	included	exserted	included	included
Style and stigma in anthesis	style as long as the corolla, included. Stigmas slightly bilobed, poorly differentiated from the styles, papillose	exserted from the corolla and from the calyx; stigma capitate	style and stigma included; stigma capitate	exserted from the corolla and from the calyx; stigma punctiform to subclavate
Length of the seeds	1.3-1.5 mm	1.6-2.1 mm	1.1-1.3 mm	1.8-2.2 mm
Distribution and altitudinal range	Santander, Boyacá, and Cundinamarca; eastern slopes of the Colombian Eastern Cordillera. 3500-4335 m	Azuay, Carchi, Chimborazo, Cotopaxi, Napo, Pichincha and Tungurahua (Ecuador; endemic, according to Molau, 1999). Peru (according to Luteyn, 1999). (3250-) 3600-4650 m	Azuay, Carchi, Chimborazo, Cotopaxi, El Oro, Imbabura, Pichincha, Tungurahua (Ecuador); Peru, Bolivia, N Argentina, N Chile. 3000-4200 m	Azuay, Bolívar, Cañar, Chimborazo, Cotopaxi, El Oro, Loja, Napo, Tungurahua (Ecuador); Peru, Bolivia. 2500-4000 m

***Castilleja paramensis* F. González & Pabón-Mora, sp. nov.** TYPE: COLOMBIA. **Boyacá**: Sogamoso, Páramo de Siscunsí, alrededores de la Laguna de Siscunsí, 3875 m, 5º22'N, 72º50'W, 04 Feb 2013 (fl), *F. González, G. Plunkett, A. Nicolas, J. Aguirre & A. Herrera 4478* (Holotype: COL; isotypes: HUA, NY, UPTC, to be distributed). Figs. 1-3

Small, rhizomatous, decumbent, perennial herbs; ascending stems to 5(-8) cm tall, branching from the base. Rhizomes very thin, whitish, with a few scattered achlorophyllous triangular scale-leaves to 2 mm long and 1 mm wide. Internodes of the aerial shoots very short, to 3 mm long. Leaves congested, sub-opposite, cucullate, sessile, broadly elliptic, to 7 mm long and 5 mm wide, entire to slightly bi- or trilobate, light green when young, later with the distal half purplish, lateral lobe(s) triangular, ascending, glabrous above, scarcely villous below, margins villous, especially along the distal half. Bracts broadly elliptic, bi- or trilobate and bright red in their distal half, glabrous above, villous below, with those subtending the mature flowers becoming purplish. Flowers subsessile, pedicel < 1 mm long, axillary to the 3-4 most distal bracts. Calices 8-11 mm long, green when immature, with bright yellow distal half at maturity, not inflated, villous, tube to 6 mm long, median clefts strongly unequal, the adaxial 1-1.5 mm deep, the abaxial 4.5-5.5 mm deep, lateral clefts absent. Corollas 8-11.5 mm long, completely included or very slightly exserted from the calices, hyaline, straight to very slightly incurved, tubes 5-6 mm long, the galeas 4-5.5 mm long, villous along the adaxial mid-line, the lower three lips consisting of bright green, extremely reduced, triangular, to 0.5 mm long and 0.2 mm wide, ascending, glabrous. Stamens included, slightly didynamous; filaments 8.5-10.5 mm long, adnate to the corolla tube for its proximal 1/3, anthers lanceolate, ca. 0.5-0.8 mm long, thecae slightly asymmetric. Styles as long as the corollas and included during anthesis. Stigmas slightly bilobed, poorly differentiated from the styles, papillose. Capsules oblong, to 10 x 5 mm, villous. Seeds obconical, 1.3-1.5 x 0.8-1 mm, seed coat papery, translucent, unruptured, with deep and narrowly hexagonal reticulation cells.

Etymology: The specific name refers to the ecosystem where the species has been found.

Distribution and phenology: *Castilleja paramensis* has so far been collected in páramos of the departments of Santander, Boyacá and Cundinamarca (Colombia). It sets flowers in September, November to March and in May, and fruits in February, June and September.

Vernacular name: "Flores de lagarto" (Güicán, Boyacá; *FG 1391*).

Additional specimens examined (when available, we have included the field notes referring to the association of the new species with *Plantago rigida*). **COLOMBIA. Boyacá:** Morrena seca 200 m NW de la Laguna Pintada, con *Espeletia colombiana* predominante, asociada con *Aciachne pulvinata*, *Agrostis breviculmis, Agrostis trichoides* y *Acaena cylindrostachya*, 3995 m, 25 Sep 1972 (fl, fr), *A. M. Cleef & P. A. Florschütz 5508* (COL); Páramo de La Rusia, NW-N de Duitama, Peña Blanca, 2 km al NE de Buenos Aires, pantanos con almohadas de *Plantago rigida* predominantes, 3720 m, 16 Dic 1972 (fl), *A. M. Cleef 7317* (COL); Sierra Nevada del Cocuy, páramo Cóncavo, superpáramo en el límite con el páramo p.d., 3.5 km al NNW del morro Púlpito del Diablo, cabeceras de vallecitos entre morrenas, protegidas a viento con un frailejonal denso y húmedo de *Espeletia lopezii*, 4335 m, 26 Feb 1973 (fl, fr), *A. M. Cleef 8530* (COL); Socotá, páramo de Pisba, sitio La Playita, entre colchones de *Plantago rigida* (*FG 824*), c 3600 m, 15 Nov 1986 (fl), *F. González et al. 823* (UPTC); Socha, sitio Los Pinos, 3600 m, asociada a *Plantago rigida (FG 1118A*), 25 Jun 1987 (fl), *F. González et al. 1118* (UPTC); Güicán, ascenso al Ritacuba Blanco, por las cabañas

del Himat, 3800-4800 m, 1 Mar 1988 (fl), *F. González et al. 1391* (UPTC); Güicán, Sierra Nevada del Cocuy, carreteable entre la cabaña del Inderena y las Lagunillas, frente a la Laguna La Atravesada, 4000 m, entremezclada con *Plantago rigida* (*FG 1417*), 2 Mar 1988 (fl), *F. González et al. 1416* (UPTC); Belén, páramo del Güina, 3500 m, 22 May 1993 (fl), *F. González & R. Small 2720* (COL, UPTC); Sierra Nevada del Cocuy, sector SE, valle del río Lagunillas, entre 3650 y 4000 m, 24 May 1993 (fl), *F. González & R. Small 2734* (COL, UPTC); Güican, ascenso hacia el Boquerón de Cardenillo, 6°18´50.6´´N, 72°12´15.6´´W, ca. 4300 m, 17 Ago 2013 (fl), *S. González et al. 01* (COL); Güicán, Sierra Nevada del Cocuy, Laguna Grande de los Verdes, en colchones de *Distichia* sp., 3900-4100 m, 20 Sep 1978 (fl, fr), *O. Rangel & H. Sturm 1534A* (COL); below the Playas of Ritacuba in the Cocuy mountains above Güicán, locally frequent in poorly drained damp paramo 3700-4500 m, particularly in damp flushes and poorly drained grassy hollows, 4200 m, 24 Jun 1984 (fl, fr), *J. R. I. Wood 4458* (COL). **Cundinamarca**: Páramo de Sumapaz, Chisacá, pantano con cojines de *Plantago rigida*, 3680 m, 11 Dic 1971 (fl), *A. M. Cleef 143* (COL); Macizo de Bogotá, páramo de Chisacá, around the lakes at about 3620 m, 16 Sep 1961 (fl), *J. Cuatrecasas & R. Jaramillo M. 25972* (COL). **Santander**: Cordillera Oriental, páramo del Almorzadero, above 3600 m, slope above ciénaga, very wet, with hummocks of mosses, *Plantago rigida*, etc., 31 Dec 1959-1 Jan 1960 (fl), *H. G. Barclay & P. Juajibioy 10369* (COL).

Castilleja paramensis is morphologically similar to *C. pumila*, *C. virgata* and especially to *C. nubigena* (Table1). It clearly differs by its smaller size (up to 8 cm), broadly elliptic and entire to slighly trilobed leaves and bracts, reduced pedicel (<1mm) and flower (0.8- 1.15 cm) lenght, bright yellow and not inflated calyx, and corolla included or very slightly (for < 2 mm) exserted from the calyx (Fig. 1). Additional differences between *C. paramensis* and *C. nubigena* include the absence of lateral clefts of the calyx (Fig. 3B, D), the straight to very slightly incurved corolla, the included stamens and the bilobed, poorly differentiated stigma in the former, *versus* the presence of lateral clefts of the calyx, the strongly incurved corolla, the exserted stamens and the capitate stigma in the latter. Finally, the presence of included corolla, stamens, styles and stigmas (Figs. 1, 3) in *C. paramensis* strongly suggests the ocurrence of cleistogamy in this species.

On the systematics and life history of *Castilleja*: The systematics of *Castilleja* has been considered difficult, mainly due to polyploidy, lack of crossing barriers among species, and effective natural hybridization, all of which can drastically change the morphological traits used to distinguish species (Heckard 1964, Heckard & Chuang 1977, Chuang & Heckard 1991, Mathews & Lavin 1998, Hersch-Green & Cronn 2009, Clay *et al.* 2012, Hersch-Green 2012). At a suprageneric level, polyploidy has also led to differential sampling of paralogs (e.g. *PHYA*) in phylogenetic analyses, resulting in a polyphyletic *Castilleja* (Bennett & Mathews 2006).

The South American species of *Castilleja* fall into two different subgenera, *Castilleja* and *Colacus*. All the Colombian species belong to the subgenus *Castilleja* (*sensu* Chuang & Heckard 1991), as the flowers are narrow and tubular, the associated bracts, the calices and/or corollas are red, and the galea is at least three times longer than the lower three lips. All these traits have been associated with hummingbird, pollination in the genus (Pennell 1948, Chuang & Heckard 1991, Heide-Jørgensen 2008). Hummingbird pollination, in turn, appears to be correlated with the evolution of perenniality in the genus (Tank & Olmstead 2008, 2009). This perennial habit has evolved once from an annual

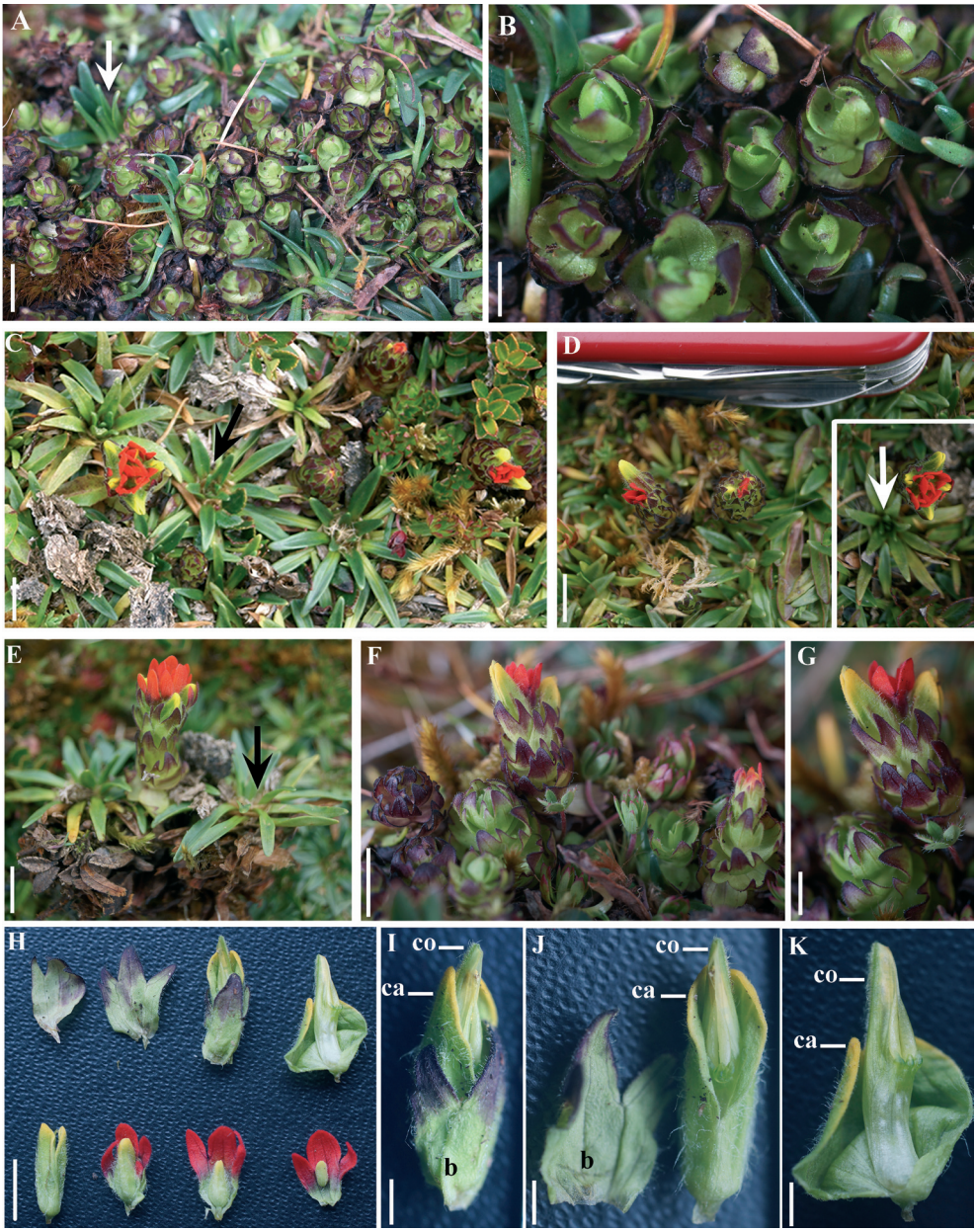

Figure 1. *Castilleja paramensis* F. González & Pabón-Mora (from the type). **A, B**. Young shoots with congested leaves. **C, D**. Flowering individuals at different developmental stages (the youngest at the upper right in **C**, the oldest at left in **D**). Inset in **D** shows a flowering shoot associated with a rosette of *Plantago rigida*. **E-G**. Flowering shoots, lateral view. **H.** Dissected flowering shoot, from left top to right bottom: basal leaf (adaxial side), mid-level leaf (abaxial side), proximal flower and subtending bract (abaxial view), flower with calyx partially removed (abaxial view), calyx (abaxial view), and three young floral buds with subtending bracts. **I-K**. Details of **H**. Arrows point to *P. rigida*. **b**, bract; **ca**, calyx; **co**, corolla. Bars: 1 cm in **A, C-F**; 5 mm in **B, G, H**; 2 mm in **I-K**.

Figure 2. **A, B**. *Castilleja paramensis-Plantago rigida* associations showing the belowground connections. **C-E.** Successive stages during establishment of belowground connections. **F, G**. Roots and stolons of *C. paramensis* showing aboveground renewal shoots and scale leaves scattered along the stolons. **H**. Isolated renewal shoot showing transition between basal scale-leaves, and emerging expanded leaves. Bars: 5 mm in **A, B, D-H**, 1 mm in **C**.

condition in *Castilleja*, and it seems to be tightly associated with polyploidy at least in the North American species (Tank & Olmstead 2008). The new species can be assigned unequivocally to subgenus *Castilleja*, and it is morphologically and ecologically similar to the high-Andean species *C. nubigena, C. pumila* and *C. virgata* (Table 1). The latter three species form a clade of perennial but primarily diploid species (Tank & Olmstead 2009). We anticipate that the perennial *C. paramensis* belongs to this clade; however, chromosome counts and molecular data are needed to confirm this placement. In addition, studies on pollination biology of *C. paramensis* are critical, as its colorful flowers are near the ground and appear to be too small and too low for hummingbird pollination. The

included style and stigma of *C. paramensis* (Fig. 3) strongly suggest that the species might be cleistogamous, despite the fact that it can co-occur with *C. integrifolia*, a species pollinated by the hummingbird *Oxypogon guerinii* (Salamanca-Reyes 2011).

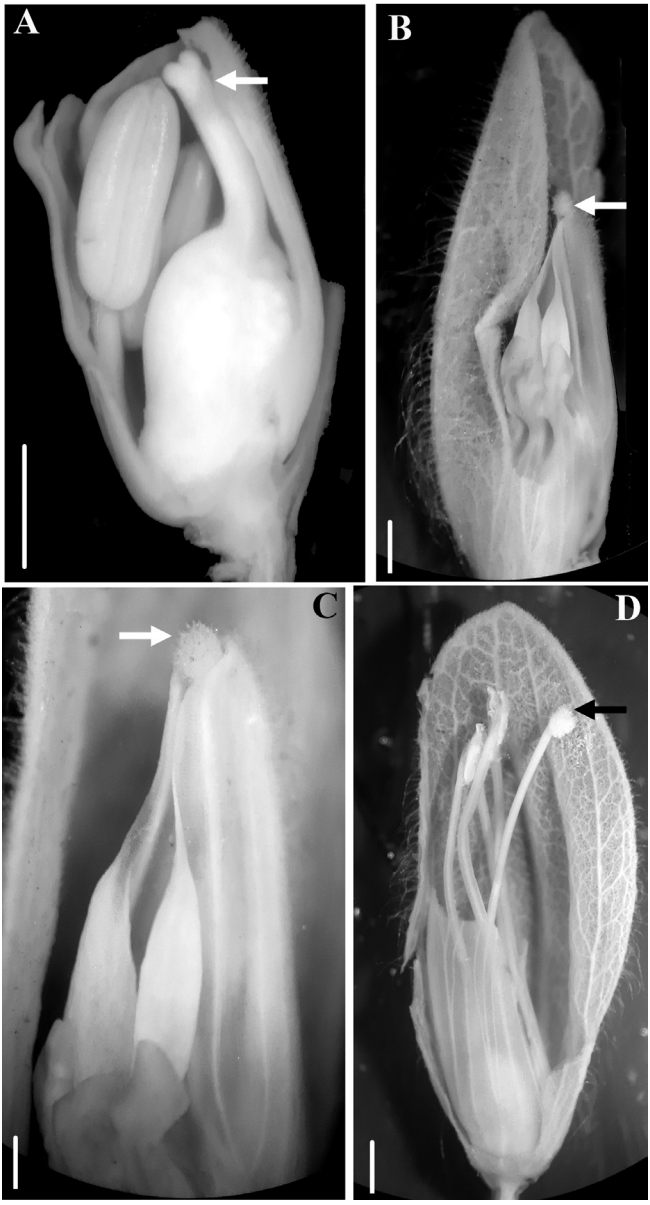

Figure 3. Dissected flowers of *Castilleja paramensis* (from *S. González 01*, COL).
A. Longitudinal section of a young flower before corolla elongation. **B**. Flower during corolla elongation, showing the stigma at the level of the tip of the galea; note the absence of lateral clefts on the calyx. **C**. Detail of **B**. **D**. Flower at late anthesis, the galea partially removed; note the included style and stigma, the latter reaching the same level of the dehisced anthers; note also (in the back) half of the calyx lacking lateral clefts. Arrows point at the stigma. Scale bars = 1 mm.

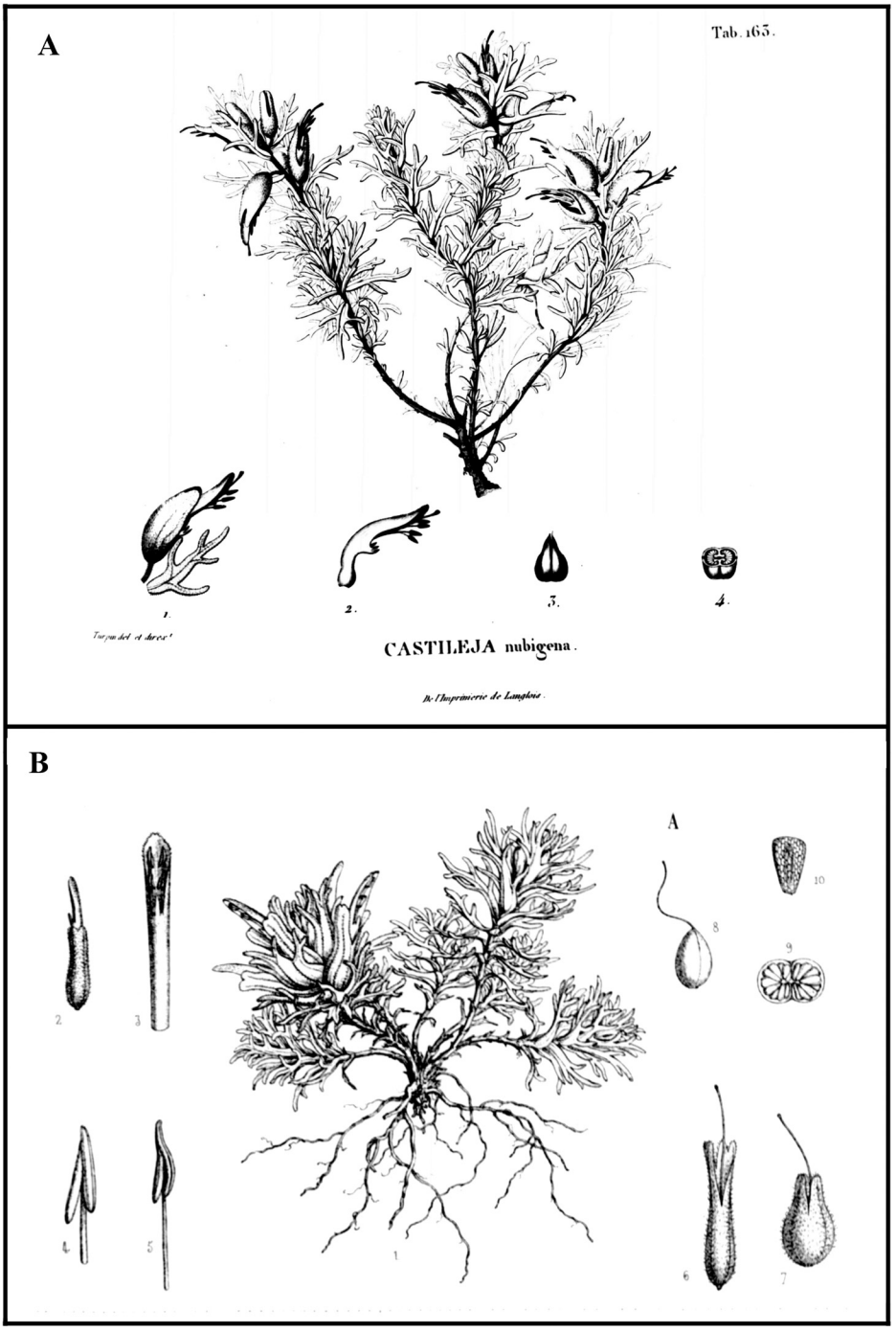

Figure 4. Original drawings of two high-Andean *Castilleja* spp. **A**. *C. nubigena* Kunth (Table 163 from Humbold, Bonpland & Kunth, 1817). **B**. *C. pumila* (Benth.) Wedd. ex Herrera (Table 61 from Weddell, 1857).

***Castilleja* species as facultative root hemiparasites.** Species of *Castilleja* are facultative root hemiparasites, which means they can complete their life cycle either as parasites or singly without a host (Heckard 1962, 1964, Matthies 1997, Heide-Jørgensen 2008, Fay *et al*. 2010). *Castilleja* host association is broad and can infect species across a diverse range of flowering plant families **(**Heckard 1962, Musselman & Press 1995), though some species might have more exclusive associations. This is the case for *C. paramensis*, frequently found associated belowground with *Plantago rigida* (Fig. 2). In fact, Cleef (1981:127) included *C. paramensis* (referred there as "*C. fissifolia* ssp. *pygmaea,* ssp. nom. herb.; in ed.?") and *P. rigida* as two primary components of the *Wernerietea* syntaxonomy that conforms the "flush vegetation and cushion bogs".

Seed germination in *Castilleja* can occur in the absence of a host (Heckard 1962); however, species from high elevations may require moist and cold conditions that can slow down germination rates (Kuijt 1969). Heckard (1962) examined hemiparasitic *Castilleja* species growing with and without hosts and noticed that generally plants growing as parasites are more vigorous, branch more profusely, and exhibit early flowering. Haustoria in *Castilleja* are small (less than 1 mm in diameter) and are not as invasive or penetrating as haustoria of other parasitic flowering plants. They initiate as elongated epidermal cells similar to root hairs (Kuijt 1969). The first responses during haustorial initiation are cortical enlargement and increasing cell division, resulting in lateral or apical protuberances in the parasite root similar to other Orobanchaceae, such as *Bartsia, Lathraea, Melampyrum, Pedicularis* and *Rhinanthus* (Heckard 1962, Dobbins & Kuijt 1973a, Weber & Weberling 1975, Riopel & Timko 1995). A mature haustorium of *Castilleja* is composed of a plate xylem zone surrounded by parenchyma, a centrally located core of collenchyma (with vessel members scattered), and the haustorial surface (Dobbins & Kuijt 1973a). Penetration is likely due to cell dissolution in the host, accompanied by crushing of cells (Dobbins & Kuijt 1973b). The haustoria of *C. paramensis* are spherical to cup-shaped and usually terminal in secondary roots.

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